THE PERCEPTION OF CHROMATIC STIMULI IN THE PERIPHERAL HUMAN RETINA*

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We have studied the changes that occur in human colour perception in the peripheral retina. By modelling the magnitude of activation produced in the L-M and S-(L+M) cone-opponent systems for matched para-foveal and peripheral chromatic stimuli, we have found that variations in perceived appearance are mirrored by a reduction in function of the L-M opponent system. The operation of the S-cone opponent system is affected to a much lesser degree, implying that there is a changing pattern of predominance between the two cone-opponent mechanisms in the peripheral retina. We will explore possible retinal and cortical bases for these changes.

Key words: *color, perception, opponent processes, central and peripheral retina.*

Introduction

Like many other aspects of visual perception, human colour vision has been shown to vary across the visual field. Numerous studies have demonstrated that when coloured stimuli are viewed at eccentric retinal locations away from the fovea, there are changes in both the perceived hue and saturation of such stimuli (Moreland & Cruz, 1959; Abramov et al., 1991; Nerger et al., 1995; Ayama & Sakurai, 2003; Parry et al., 2006; McKeefry et al., 2007). These changes in colour perception have been variously attributed to changes in the cone photoreceptor density with increasing retinal eccentricity (Gordon & Abramov, 1977) or to the increasing influence of rods (Stabell B., &

Stabell U., 1996). More recently, attention has focussed on the possibility that there may be re-organisation of cone inputs into peripheral retinal ganglion cells which results in losses in cone opponent function. Human behavioural studies have demonstrated differential losses in sensitivity between the L-M and S-(L+M) cone opponent mechanisms, with the former becoming more functionally compromised than the latter with increasing retinal eccentricity (Mullen & Kingdom, 2002; Mullen et al., 2005; Murray et al., 2006).

The formation of cone-opponent mechanisms forms a crucial stage in the processing of colour information in the primate visual system. They arise at the level of the retinal ganglion cells where outputs form the long- (L), middle- (M) and short-wavelength (S) sensitive cones are combined in a subtractive or opponent manner. Information in the L-M cone-opponent pathway is mediated by the midget ganglion cells (MGC) whilst S-(L+M) opponency is carried by specialised midget bipolars and bi-stratified ganglion cells (Dacey & Lee, 1994). Currently, there are conflicting views regarding how the nature of the L- and M-cone inputs to the centre and surrounds of the MGC receptive fields changes from the fovea to the peripheral retina. One school of thought suggests that the losses in L-M opponent function that occur with increasing retinal eccentricity are due to losses in the cone specific inputs to the centres and surrounds to the MGCs. In the parafoveal retina, MGC receptive field centres receive input from a single specific cone (e. g., an L-cone). The receptive field surrounds may, in accord with the 'cone selective hypothesis' (Reid & Shapley, 1992; Lee et al., 1998; Martin et al., 2001), receive input from a different cone type (e.g., an M-cone), or alternatively receive input from mixed cone types according to the 'random

wiring hypothesis' (Lennie et al., 1991; Dacey, 1996; 2000; Mullen & Kingdom, 1996). Regardless of whether cone inputs are organised in selective or random fashion, cone opponency exists in the central retina by virtue of the fact that the centres receive input from a single type of cone. In the retinal periphery there is an increase in receptive field size and, as a consequence of this, both the centres and surrounds receive input from multiple cones. If cone selectivity is maintained (i.e. if central input is either all M-cone or all L-cone), then cone opponent function will be preserved. If, however, cone inputs follow a more random pattern in the periphery (i.e. there is mixed L- and M-cone input), this will result in the loss of cone-opponent function.

In this study, our aim is to characterise the perceived changes in appearance that occur when coloured stimuli are presented in more peripheral regions of the retina, in an attempt to examine how peripheral colour perception compares with that at the fovea. In so doing we wish to gauge to what extent these shifts in perception are mediated by differential losses in function of the L-M and S-(L+M) cone opponent mechanisms. Furthermore, we wish to assess what the implications are of these shifts in colour perception in relation to the circuitry of cone opponency in the peripheral retina.

Methods

Circular test patches of variable size were generated on a Sony GDM520 CRT display using a VSG 2/5 (Cambridge Research Systems, Rochester, UK) and purpose-built software. The monitor frame rate was 120 Hz, and calibration was performed with a PR650 spectrophotometer (Photo Research, Chatsworth, CA). Stimuli were defined in a modified

MacLeod-Boynton colour space described by A. M. Derrington et al. (1984). To measure the perceived changes in colour when stimuli are presented in the peripheral visual field, an asymmetric matching paradigm was used. A 1° diameter probe stimulus was presented 1° nasal to fixation, and at the same time the test stimulus was presented along the same horizontal meridian, but at a greater nasal eccentricity. Both targets were presented for 380 ms. Background chromaticity in CIE 1931 space was $x = 0.31$, $y = 0.316$ (illuminant C). Depending upon the experiment, observers used either a same/different matching paradigm or a method of adjustment to match the test and the probe for hue and saturation. The probe was presented over a range of chromatic axes which sampled across 360 degrees of

colour space at 15-deg intervals (see Figure 1). The initial test patch appeared at the same hue and luminance ($12.5 cd/m^2$) as the probe. After each adjustment, there was a 500 ms period before the modified test setting appeared. Subjects pressed a button to change the probe hue when they were satisfied with the match.

In order to model the colour matching data in the context of cone opponency, we have used a photoreceptor-to-mechanism transformation originally described by R. Stanikunas et al. (2005) and used subsequently by I. J. Murray et al. (2006). The model is based on linear interactions between the three L-, M-, and S-cone types, and cone excitations (L, M and S) generated by the colour stimuli are computed using their CIE 1931 chromaticity co-ordinates in conjunction with the fundamentals of
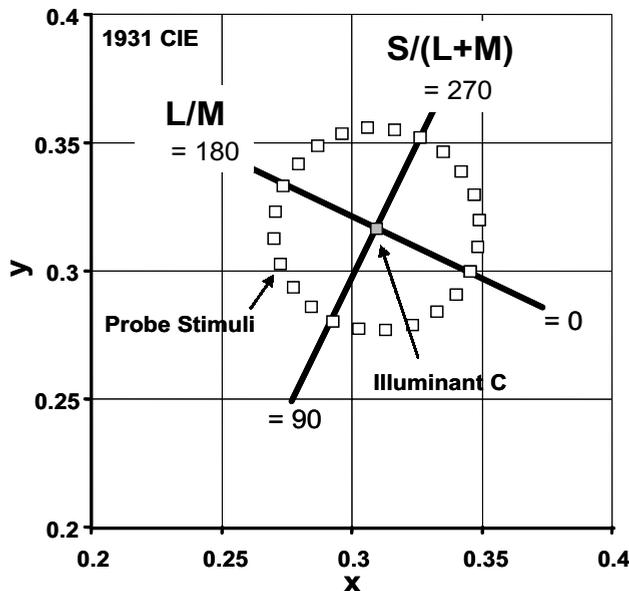
Figure 1. *Location in 1931 CIE chromaticity space of the probe and test stimuli that were used in the colour matching experiments. The stimuli sampled a 360°, colour circle which was centred on illuminant C ($x = 0.31$, $y = 0.316$). Stimulus hue could be manipulated by adjusting the azimuth (ϕ) in this colour space. The L-M cone opponent channel was isolated by stimuli where $\phi = 0$ or 180°. The S-(L+M) opponent channel was isolated by stimuli where $\phi = 90$ or 270°. Stimuli in between these cardinal axes activated both opponent channels to varying degrees.*

V. C. Smith & J. Pokorny (1975) (see Wyszecki & Stiles, 1982). Cone opponent outputs (L-M) and (S-(L+M)) and achromatic outputs (L+M) are calculated as follows (Equation 1):

$$\begin{bmatrix} L+M \\ L-M \\ S-(L+M) \end{bmatrix} = \begin{bmatrix} 0.63 & 0.395 & 0 \\ 2.21 & -2.6 & 0 \\ 0.35 & 0.35 & -1.02 \end{bmatrix} \begin{bmatrix} L \\ M \\ S \end{bmatrix} \quad (1)$$

The cone fundamentals are normalized with respect to illuminant C. The criteria for choosing the co-efficients for this transformation were as follows: i) luminance is based on a ratio of 1.6 between L and M, ii) opponent functions are zero for illuminant C, and iii) opponent functions are assumed to be orthogonal to each other; that is, the L-M function will have zero response at violet and cardinal yellow and the S-(L+M) function should have zero response at cardinal red and green.

Results

In order to examine how perceived hue was affected by retinal eccentricity, we employed the asymmetric matching paradigm to measure these shifts for different hues in colour space. In Figure 2, these shifts are plotted in terms of the vector rotation needed to make the peripherally presented test stimulus match the probe stimulus placed at 1 degree nasal to the fovea. As can be observed, the hue shifts generally increase with increasing eccentricity, but the magnitude of hue shift as a function of retinal eccentricity is not the same for all hues, with some chromatic axes appearing to undergo much larger perceived shifts than others.

The data exhibit prominent peaks and troughs, indicating the areas of colour space where the maximum shifts in perceived hue
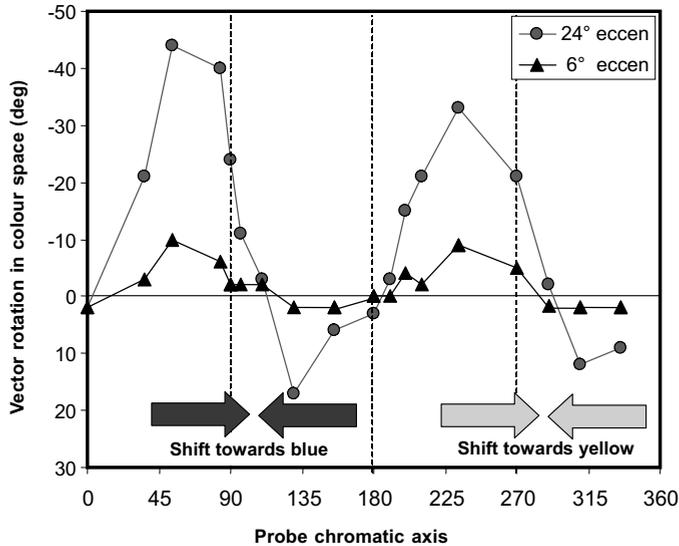
*Figure 2. **The magnitude of hue shift (given in term of azimuth rotation necessary to provide a match) produced as a function probe chromatic axis for test stimuli placed at retinal eccentricities of 6 and 24°. Note how the magnitudes of hue shift are not constant across colour space and depending on the half of the colour circle the stimulus lies in. The nature of the hue shift can be characterised as either towards blue or towards yellow.***

occur. In essence, the shifts in hue with eccentricity can be simply characterised as being either towards blue or yellow. In the pink/purple region of colour space ($\phi = 0$–$90º$), a negative (anti-clockwise) rotation of the test stimulus hue vector is required in order to make a match with the more centrally located test stimulus. This means that the more peripheral test stimulus has to be made more pink in order to counteract its perceived shift towards blue. The magnitude of this shift appears to reach a maximum between 45–$70º$ in this colour space. In the blue/green region ($\phi = 130$–$165º$), the peripheral stimulus requires a positive (clockwise) rotation of the hue vector in order to match the central probe stimulus. Once again this indicates that the more eccentrically located test stimulus is being perceived as more blue and consequently has to be made greener in order to produce a match. In the second half of the colour circle

($\phi = 180$–$360º$) the perceived shifts in hue are towards yellow. In the green region of colour space ($\phi = 220$–$260º$) large negative rotations are required for matching, i.e. the peripheral test stimulus has to be made more green/blue in order to counteract the tendency for it to be perceived as yellow. Smaller positive rotations are required in the orange/pink region ($\phi = 290$–$360º$).

In order to describe more fully the changes that occur in colour appearance with increasing retinal eccentricity, changes in perceived saturation have to be measured in conjunction with changes in perceived hue. To this end, we used a modification of the asymmetric colour matching paradigm in which observers matched peripherally presented colours with central probes having independent control of both hue and saturation. The peripheral and central colours were matched using a method of adjustment procedure. Figure 3 plots the
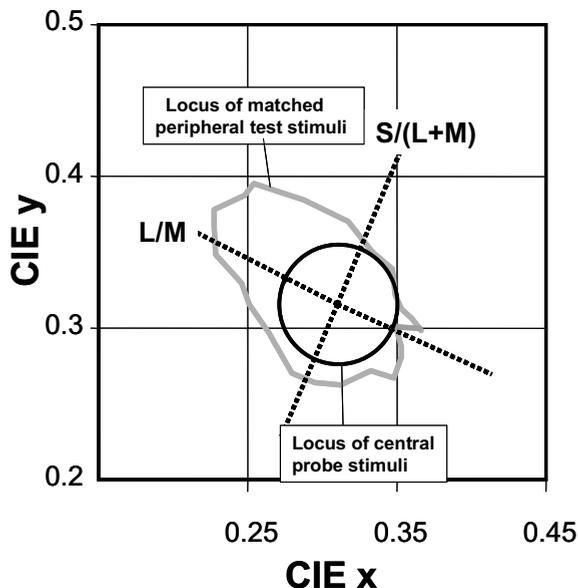
*Figure 3. **The position on the 1931 CIE chromaticity diagram of the locus of central probe stimuli (black circle) compared to the position of the peripherally test stimuli (grey line) which were matched with the central stimuli. The data are shown for a single observer (DM) for a test stimuli placed at a retinal eccentricity of 18°.***

results from a single subject who performed this experiment. The figure plots the probe and test stimuli in terms of their chromaticity co-ordinates in 1931 CIE colour space. The inner circular line is the locus of the probe stimuli, whilst the dotted outer line represents the positions of the peripheral matched stimuli. Using the chromaticity co-ordinates in conjunction with the Smith Pokorny (1975) cone fundamentals, we can compute the magnitude of L-, M- and S-cone excitations produced by the stimuli. These values can then be used in equation (1) to provide a measure of the 'output' in the second-stage cone-opponent mechanisms elicited by the probe and test stimuli.

These computations have been performed for the data shown in Figures 4a and yb). These data represent the average of 9 observers who performed the hue and saturation matching tasks for peripheral stimuli placed at a retinal eccentricity of 18°. The dotted lines show the extent to which the probe stimuli activate the S-(L+M) (Figure 4a) and L-M (Figure 4b) cone-opponent mechanisms. The solid lines show the extent to which the matched peripheral stimuli activate these cone opponent mechanisms. As can be observed, for the S-cone driven opponent mechanism both the central probe and peripheral test stimuli produce very similar levels of activation for this mechanism. This indicates that the shift of chromatic stimuli to 18° of retinal eccentricity has little effect on the operation of this cone opponent mechanism. For the L-M opponent channel, on the other hand, the levels of activation produced by the peripherally matched test stimuli are very different to those produced by the probe stimuli. In order for the peripheral test stimuli to be matched with the central probes there has to be an increase in the extent to which they have to activate the L-M opponent mechanism. Note that this is a compensatory increase which has to take place in order to negate the loss in function that
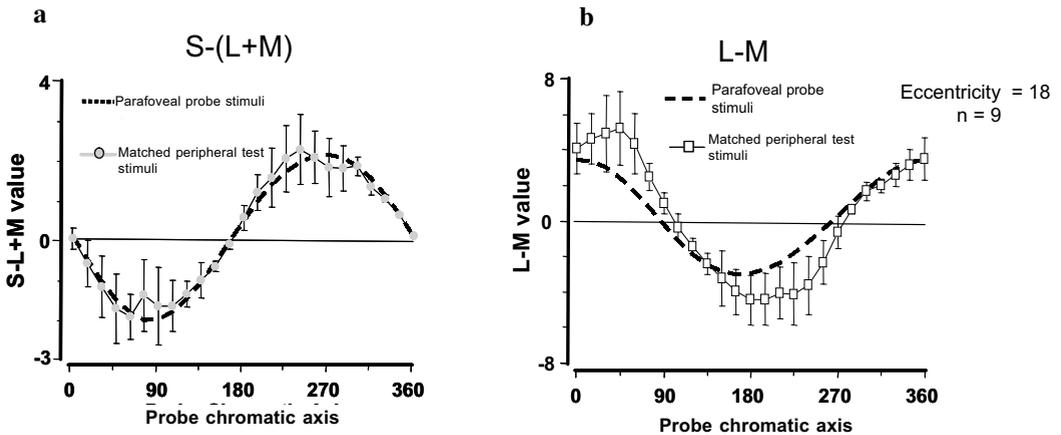
Figure 4. Averaged data for 9 colour normal observers who matched test stimuli at an eccentricity of 18° with centrally place probes. The data show the level of activations generated in the S-(L+M) cone opponent mechanism (left-hand panel) and the L-M mechanism (right-hand panel) by the probe stimuli (dotted lines) and the matched peripheral test stimuli (solid lines). The magnitudes of opponent function where computed using Equation 1.

appears to occur for the L-M cone opponency with increasing retinal eccentricity.

This differential loss in output between the L-M and S-cone driven opponent mechanisms can be seen in Figure 5 where the relative activations produced by the probe and test stimuli are shown for matched stimuli made by a single observer at eccentricities of 6, 12, 18, 20 & 24° of retinal eccentricity. As can be observed, even at the lowest eccentricities there already appears to be a loss in output from the L-M cone opponent mechanism with increased levels of activation being required for the peripheral stimuli in order to match them with the central stimuli. This becomes even more manifest at larger eccentricities, with the probe stimuli having to undergo increasingly larger compensatory increases in L-M opponent output to make up for the loss in its functionality. In comparison, the output of the S-(L+M) remains robust (i.e. similar to that of the probe stimuli) for the central 20 degrees after which it too suffers fro a loss in output.
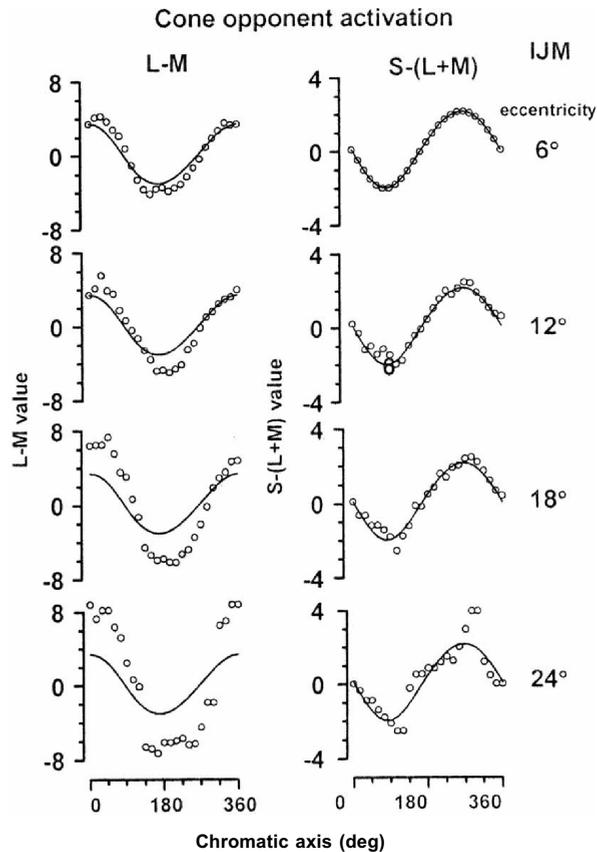
Figure 5. The magnitudes of L-M (left) and S-(L+M) (right) cone-opponent activation produced by peripherally matched test stimuli at different retinal eccentricities. Note how the levels of activation produced by the central probe stimuli (solid lines) and the peripherally matched test stimuli (empty circles) are very similar for the S-(L+M) opponent mechanism (but not for the L-M) up to 18° of retinal eccentricity. The data are obtained form a single subject (IJM).

Discussion

The main finding arising from this series of experiments is that in the peripheral retina changes in colour perception are mirrored largely by changes in the functional capacity of the L-M cone opponent system which becomes more compromised with increasing retinal eccentricity. This is in stark contrast to the opponent system that is driven by S-cone input which, at least within the central 20° of the retina, is remarkably resistant to the problems imposed on colour processing in the peripheral retina. This notion of differential losses in function between the two cone-opponent systems with increasing retinal eccentricity is consistent with ideas suggested previously (Mullen & Kingdom, 2002; Mullen et al., 2005). Furthermore, it is consistent with the notion that L-M opponent colour vision is a specialisation of central foveal vision (Mullen & Kingdom, 1996). However, whilst we agree with view of changing degrees of prominence in the peripheral retina between the L-M and S-cone driven opponent mechanisms, where we differ from the ideas put forward by K. T. Mullen and co-workers is in the nature of the losses in opponent function, particularly L-M opponent function. Our standpoint is that losses in L-M opponency with increasing retinal eccentricity are imposed centrally (i.e. at a cortical level) rather than occurring as a result of retinal based changes in the circuitry of colour neurophysiology. The latter view has been put forward by those who suggest that colour opponency is compromised by the random nature of L- and M-cone input to midget ganglion cells (MGC) in the retinal periphery (Mullen & Kingdom, 2002; Diller et al., 2004). We argue for a central basis for these changes in peripheral colour perception, and this argument is based upon the results from spatial scaling experiments that we have performed in our laboratory (Vakrou et al., 2005). These experiments compared L-M and S-(L+M) chromatic sensitivity in the fovea and peripheral regions of the retina and demonstrated that any measureable deficits in L-M opponent function can be negated simply by appropriate increases in stimulus size. This result is important because it demonstrates that chromatic sensitivity is actually preserved in the peripheral retina, and thus cone selective L- and M-cone inputs to the centres and surrounds of MGC must be preserved. It implies that observed differences between the L-M and S-(L+M) opponent mechanisms are due to different cortical magnification factors for the two mechanisms (Vakrou et al., 2005).

One might have thought that anatomical and physiological evidence obtained directly from the retina would be able to resolve unequivocally the issue as to whether changes in peripheral colour perception arise as a consequence of retinal or cortically imposed constraints. Unfortunately, this is not the case. Conflicting results from physiological experiments echo the contradictory findings from human psychophysics. For example, work by P. R. Martin et al. (2001), who have studied MGC properties, has shown that there is little effect on L-M chromatic sensitivity up to about 40° of retinal eccentricity. So this lack of variation observed in chromatic sensitivity, expressed by opponent ganglion cells away from the fovea, cannot be readily explained by changes at the ganglion cells level. On the other hand, studies by L. Diller et al. (2004) have shown that the quality of the L-M cone opponent signal is definitely reduced in the retinal periphery – supporting more retinal-based reasons for changes in peripheral colour vision.

Perhaps some form of compromise between the distal (i.e. retinally imposed) versus

central (i. e. cortically imposed) theories for changes in colour perception in the periphery might be found in recent work by S. G. Solomon et al. (2005). They have found that there may well be some reduction in the quality of L-M opponent signals in peripheral retina and suggest this may be due partly to three factors: the temporal characteristics of the pre-ganglionic cell synaptic circuits, eccentricity-dependent increases in delay between centre and surround responses, as well as a reduction in the overall number of cells showing overt opponent responses. At the same time, however, they stress that, despite this reduction in the quality of cone opponency in the periphery, there are no physiologically measurable differences in sensitivity between central and peripheral L-M opponent cells. Hence we might speculate that, whilst absolute sensitivity to chromatic stimuli might be restored by adequate size scaling as has been shown by C. Vakrou et al. (2005), the hue or colour appearance of supra-threshold stimuli, on the other hand, might be affected to a greater extent by this loss of quality of the opponent signal. This view is supported by the fact that measured changes in perceived hue shifts with increased retinal eccentricity remain, despite increases in stimulus size (Parry et al., 2006), thus suggesting that colour appearance may not be size-scaled like chromatic sensitivity.

In conclusion, we have shown that the changes that we perceive in our colour perception for stimuli placed in our peripheral visual field are largely due to losses in function of the L-M cone opponent system. Further work will be necessary in order to resolve the ongoing debate as to whether these losses in cone opponent function are due to changing cone input at the retinal ganglion cell level or, on the other hand, due to cortically imposed limitations on the processing of colour information.

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SPALVOTO STIMULO SUVOKIMAS REGIMOJO LAUKO PERIFERIJOJE

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S a n t r a u k a

Mes tyrėme, kaip pakinta stimulo spalvos suvokimas, kai stimulas matomas regimojo lauko centre ir kai periferijoje. Lygindami L-M ir S-(L+M) oponentinių sistemų, gaunančių signalus iš centrinės ir periferinės tinklainės dalies, aktyvumą, nustatėme, kad spalvų suvokimo pokyčiai atspindi L-M oponentinės sistemos aktyvumo silpnėjimą periferijoje. S kūgelių įtaka oponentinės sistemos aktyvumui kinta mažiau negu L-M kūgelių. Taigi, dviejų oponentinių sistemų santykinė įtaka spalvos suvokimui periferijoje ir centre pakinta. Straipsnyje tiriama, kokią reikšmę šiems pokyčiams turi tinklainėje ir smegenų žievėje vykstantys procesai.

Pagrindiniai žodžiai: spalva, suvokimas, oponentinės ląstelės, centrinė ir periferinė tinklainė.